A revision of *Haplocaulus* Precht, 1935 (Ciliophora: Peritrichida) and its morphological relatives

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Synopsis

The species of *Haplocaulus* and of five closely related genera have been revised. A diagnosis for each genus is given with a key to its constituent species. Two new genera, *Piesika* n. gen. and *Pseudohaplocaulus* n. gen. are described. All extant species are described and figured. These include *Haplocaulus*—of which 26 species are recognised; *Baikalonis*—3 species; *Cotensita*—1 species; *Parazoothamnium*—2 species; *Piesika*—1 species; *Pseudohaplocaulus*—2 species. Two other genera, *Monintranstylum* and *Tucolesca*, are also considered.

Introduction

In two previous papers (Warren, 1986, 1987) the peritrich genera *Vorticella* and *Pseudovorticella* were revised. Both are solitary forms the stalks of which coil up in a helical fashion upon contraction. The genera dealt with in this paper are also solitary and borne on unbranched contractile stalks but, upon contraction, the stalks do not coil helically.

Two of the principal generic characters used here are the mode of stalk contraction and the presence of pellicular tubercles with their underlying reticulate silverline system. Nevertheless for some species, details concerning these characters are not available. For example, with the exception of *Haplocaulus terrenus*, no species of the genera reviewed have been impregnated with silver—the possession of reticulate silverline systems has been assumed from the presence of pellicular tubercles. However, although pellicular tubercles are usually associated with reticulate silverline systems, this may not be true in every case (Foissner, pers. comm.).

The major genus included here is *Haplocaulus* Precht, 1935 which is found in marine, freshwater and terrestrial habitats attached to plant, animal and inanimate substrates. The only previous revision of *Haplocaulus* was that of Stiller (1971); seven new species have since been described and several species have been transferred from other genera. *Baikalonis*, *Cotensita* and *Parazoothamnium*, three genera closely related to *Haplocaulus*, are revised and two new genera, *Piesika* and *Pseudohaplocaulus*, are described. All extant species are described and figured and keys to their identification are provided. A brief account of the morphological structures important in the taxonomy of the Vorticellidae is given in Warren (1986).

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Key to genera

1	Zooid with pellicular tubercles	2
–	Zooid without pellicular tubercles	3
2	Stalk contracts in two stages, initially shortening in a concertina-like fashion and then bending in a zigzag manner	*PIESIKA*
–	Stalk contracts in zigzag manner only	*PSEUDOHAPLOCAULUS*
3	Stalk sheath folded below zooid	*COTENSITA*
–	Stalk sheath not folded below zooid	4
4	Upon contraction stalk shortens longitudinally and is enveloped by zooid	*BAIKALONIS*
–	Contraction does not result in zooid enveloping stalk	5
5	Stalk contracts in two stages, initially shortening in a concertina-like fashion and then bending in a zigzag manner	*PARAZOOTHAMNIUM*
–	Stalk contracts in zigzag manner only	*HAPLOCAULUS*

Genus *HAPLOCAULUS* Precht, 1935

The genus *Haplocaulus* was erected by Precht (1935) to include solitary vorticellids whose stalks are circular in cross-section and which contract in a zigzag rather than helical fashion. Impregnation by silver reveals a pattern of equally spaced horizontal lines or striations which encircle the body. These striations may or may not be visible in the living zooid.

Two species were originally described by Precht (1935), *H. nicoleae* and *H. furcellariae*, although he failed to designate either as the type. *H. nicoleae* is here transferred to the genus *Pseudohaplocaulus*. *H. furcellariae* is designated the type species. Stiller (1971) transferred ten species to *Haplocaulus* all of which had previously belonged to the genus *Vorticella*. Three more vorticellids are here assigned to *Haplocaulus* for the first time.

DIAGNOSIS. Zooid borne upon an unbranched stalk which is circular in cross-section and contracts in a zigzag manner. Zooids usually oval, cylindrical or inverted bell-shaped. Impregnation by silver reveals a transverse silverline system. Spasmoneme lies either parallel to the walls of the stalk sheath or is slightly twisted in the form of a shallow helix.

Key to the species of *Haplocaulus*

1	Diameter of peristomial lip greater than or equal to maximum body width	2
–	Diameter of peristomial lip less than maximum body width	15
2	Pellicular striations visible on live zooid	3
–	Pellicular striations not visible on live zooid	10
3	Zooid elongate and cylindrical in shape	4
–	Zooid either cone- or inverted bell-shaped	8
4	Pellicle with knob-like projections	*H. eforianus*
–	Pellicle without knob-like projections	5
5	Zooid with two contractile vacuoles	*H. dipneumon*
–	Zooid with one contractile vacuole	6
6	Zooid with distinct, broadly spaced striations	*H. fluviatilis*
–	Zooid with fine, narrow-spaced striations	7
7	Macronucleus C-shaped and situated in anterior part of zooid	*H. procerus*
–	Macronucleus irregular and situated in centre of zooid	*H. furcellariae*
8	Zooid inverted bell-shaped with constriction beneath peristome	9
–	Zooid cone-shaped, not constricted beneath peristome	*H. conosomus*
9	Macronucleus lies horizontally in anterior part of zooid	*H. epizoicus*
–	Macronucleus lies longitudinally in centre of zooid	*H. distinguendus*
10	Zooid elongate, length at least × 3 maximum body width	11
—	Zooid length less than × 3 maximum body width	12
11	Upon contraction, zooid assumes characteristic nodding position	*H. crassicaulis*
—	Upon contraction, zooid remains vertical	*H. extensa*
12	Zooid with endosymbiotic zoochlorellae	*H. sertulariarum*
—	Zooid without endosymbiotic zoochlorellae	13
13	Zooid cone-shaped, not constricted beneath peristome	*H. pelagicus*
—	Zooid inverted bell-shaped, usually with constriction beneath peristome	14

14	Pellicular granules present	***H. leanderi***
—	Pellicular granules absent	***H. elegans***
15	Pellicular striations visible on live zooid	16
—	Pellicular striations not visible on live zooid	21
16	Striations distinct and widely spaced	17
—	Striations fine with narrow spacing	18
17	Pellicle with concave ribbing between striations	***H. terrenus***
—	Pellicle with convex ribbing between striations	***H. kahlii***
18	Zooid elongate, length at least × 2 maximum body width	19
—	Zooid rotund, length less than × 2 maximum body width	20
19	Macronucleus U-shaped; spasmoneme extends full length of stalk	***H. fusiformis***
—	Macronucleus C-shaped; spasmoneme does not extend complete stalk length	***H. claudicans***
20	Marine; epizoic on the echinoderm *Amphiurae squamata*	***H. amphiurae***
—	Freshwater; epizoic on the amphibian *Rana temporaria*	***H. longinucleatus***
21	Zooid elongate, length at least × 2 maximum body width	22
—	Zooid length less than maximum body width	24
22	Macronucleus spirally twisted and lies longitudinally in zooid	***H. macronucleatus***
—	Macronucleus C-shaped and lies horizontally in zooid	23
23	Zooid 134—155 μm long; epizoic on the amphibian *Rana temporaria*	***H. amphibiarum***
—	Zooid 60 μm long; epizoic on the crustacean *Gammarus pulex*	***H. stilleri***
24	Macronucleus C-, S-, or irregular in shape; infundibulum reaches at least one-third zooid length	25
—	Macronucleus J-shaped; infundibulum less than one-third zooid length	***H. walteri***
25	Macronucleus S-shaped or irregular; stalk about equal to body length	***H. brehmi***
—	Macronucleus C-shaped or irregular; stalk up to × 2 body length	***H. carinogammari***

Species descriptions

Haplocaulus furcellariae Precht, 1935

DESCRIPTION (Fig. 1). The zooid of this, the type species is elongate, almost cylindrical in shape, approximately 98 μm long × 40 μm wide. Peristomial lip 50–55 μm in diameter. Disc convex. Contractile vacuole small and situated in the peristomial region. Macronucleus elongate and irregular in shape. Pellicle with distinct transverse striations. Stalk up to 400 μm long.

HABITAT. Marine, originally found as an epizoite of *Furcellaria*.

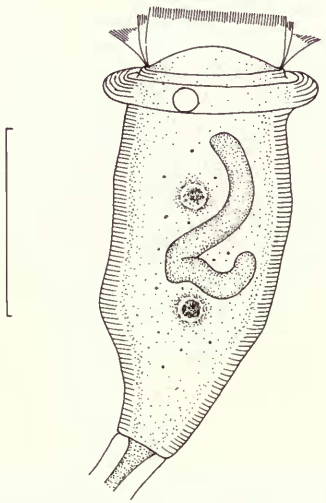

Fig. 1 *Haplocaulus furcellariae*, after Precht, 1935. Bar = 50 μm.

Haplocaulus amphibiarum Banina, 1982

DESCRIPTION (Fig. 2). Zooid 134–155 μm long × 52–65 μm wide, tapering at both ends and widest in the central region. Diameter of peristomial lip less than maximum body width. Disc cone-shaped and prominent. Infundibulum reaches one-third body length. Contractile vacuole situated in upper half of zooid. Macronucleus C-shaped and lies horizontally across centre of body. Food vacuoles often numerous and spindle-shaped. Stalk less than body length.

HABITAT. Freshwater, originally found near Leningrad, U.S.S.R. attached to the amphibian *Rana temporaria*.

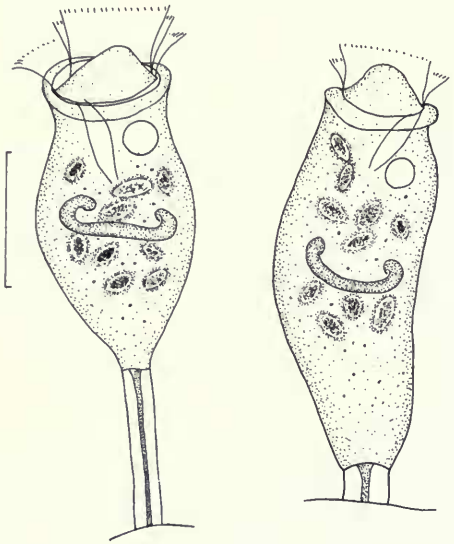

Fig. 2 *Haplocaulus amphibiarum*, after Banina, 1982. Bar = 50 μm.

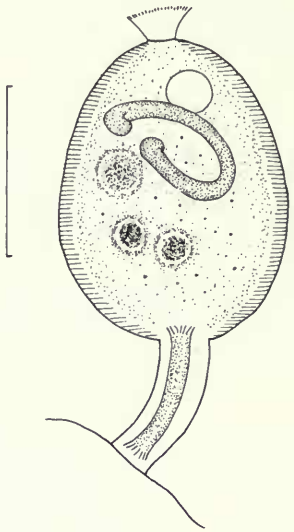

Fig. 3 *Haplocaulus amphiurae*, after Cuénot, 1891 (called *Vorticella amphiurae*). Bar = 25 μm.

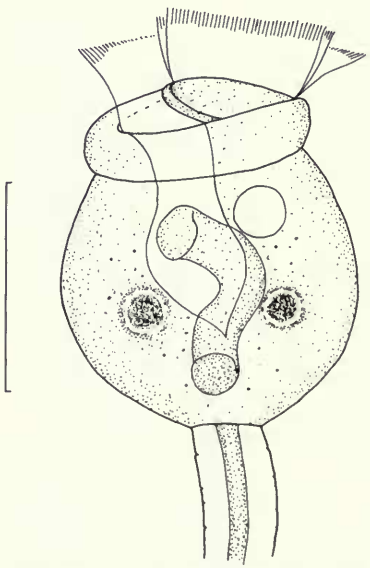

Fig. 4 *Haplocaulus brehmi*, after Lüpkes, 1975. Bar = 50 μm.

NOTE. *H. amphibiarum* bears a strong morphological similarity to *H. fusiformis* (Nenninger, 1948) Stiller, 1971 and to *Carchesium amphibiarum* Nenninger, 1948 which are also epibionts of amphibians. It is possible that these three species may be synonymous.

Haplocaulus amphiurae (Cuénot, 1891) n. comb.

Vorticella amphiurae Cuénot, 1891

DESCRIPTION (Fig. 3). Zooid 40 μm long × 25–30 μm wide, oval in shape, rounded posteriorly and with a narrow peristome. Contractile vacuole situated in upper one-third of body. Macronucleus C-shaped or occasionally irregular. Pellicle with fine transverse striations. Stalk less than body length.

HABITAT. Marine, originally isolated from the Bay of Naples as an epizoite of the echinoderm *Amphiurae squamata.*

NOTE. *H. amphiurae* is morphologically similar to *Baikalonis.* The original description of *H. amphiurae*, however, was made from partially contracted specimens. In order to determine the correct taxonomic position of this species, a redescription based on observations of healthy living specimens is required.

Haplocaulus brehmi Lüpkes, 1975

DESCRIPTION (Fig. 4). Zooid oval in shape, 80 μm long × 70 μm wide. Peristomial lip well developed, 50 μm in diameter. Disc slightly convex. Infundibulum broad and reaches two-thirds body length. Contractile vacuole situated just below the peristome. Macronucleus S-shaped or irregular, and lies longitudinally with respect to the major body axis. Pellicular striations not observed. Stalk about equal to body length.

HABITAT. Freshwater, originally found attached to the gills of larvae of the caddis-fly *Agapatus.*

Haplocaulus carinogammari Stiller (1963), 1971

Vorticella carinogammari Stiller, 1963

DESCRIPTION (Fig. 5). Zooid inverted bell-shaped, rounded, 45–75 μm long. Peristomial lip well developed, diameter about equal to maximum body width. Disc convex. Infundibulum narrow and reaches centre of zooid. Contractile vacuole situated just beneath peristome. Macronucleus elongate and irregular in shape. Pellicular striations visible on fixed specimens. Stalk up to × 2 body length.

HABITAT. Freshwater, originally found attached to the crustaceans *Carinogammarus roeselii* var *triacanthus* and *Gammarus fossarum*; also occurs on *Rivulogammarus* (Piesik, 1975) and *Asellus aquaticus* (Szczepanowski, 1978).

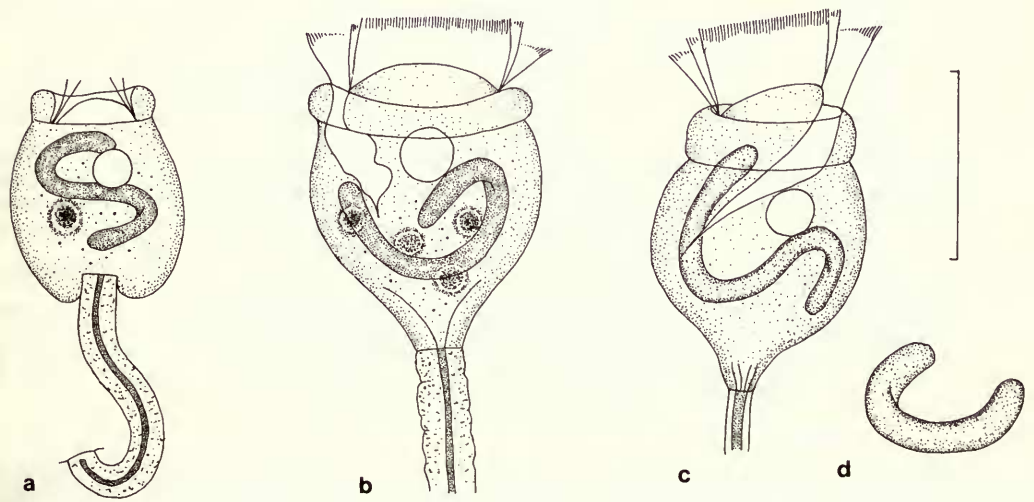

Fig. 5 *Haplocaulus carinogammari* (a) contracted; (b) relaxed, after Stiller, 1963 (called *Vorticella carinogammari*); (c) & (d) showing variation of macronucleus, after Szczepanowski, 1978. Bar = 50 μm.

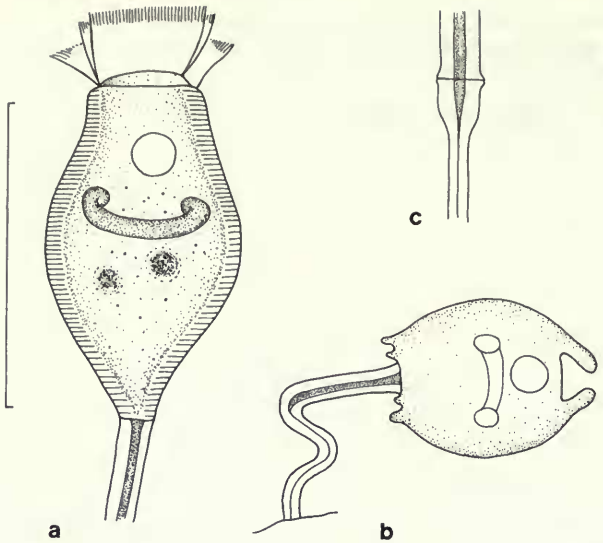

Fig. 6 *Haplocaulus claudicans,* (a) relaxed zooid; (b) contracted zooid; (c) detail of stalk, after Penard, 1922 (called *Vorticella claudicans).* Bar = 25 μm.

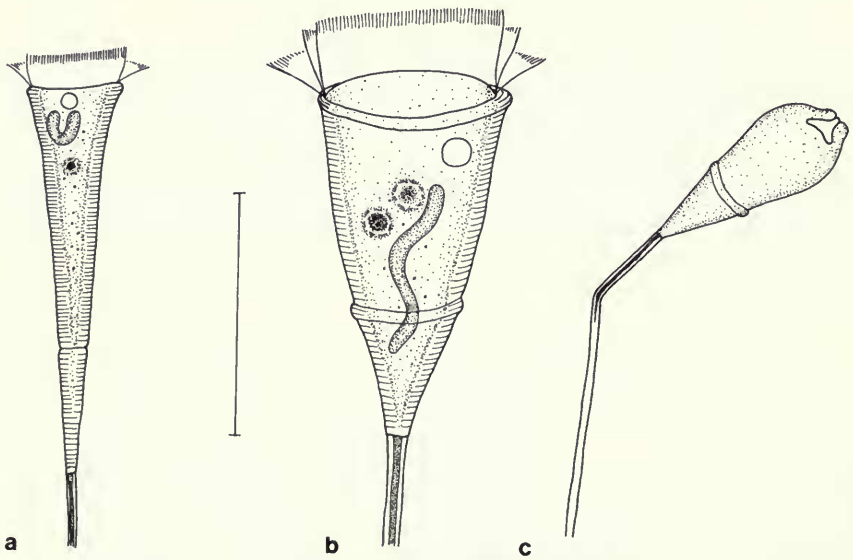

Fig. 7 *Haplocaulus conosomus,* (a) after Stokes, 1889 (called *Vorticella conosoma);* (b) relaxed zooid; (c) contracted zooid, after Gajewskaja, 1933 (called *Vorticella conesoma).* Bar = 50 μm.

Haplocaulus claudicans (Penard, 1922) Stiller, 1971

Vorticella claudicans Penard, 1922

DESCRIPTION (Fig. 6). Zooid elongate, almost cylindrical in shape, 40–55 μm long × 30 μm wide. Diameter of peristomial lip less than or occasionally equal to maximum body width. Contractile vacuole situated in upper one-third of body. Macronucleus C-shaped and lies horizontally across centre of zooid. Pellicle with fine transverse striations. Stalk about equal to body length. Spasmoneme terminates about half-way down the stalk and is connected to the base of the stalk by a fibre.

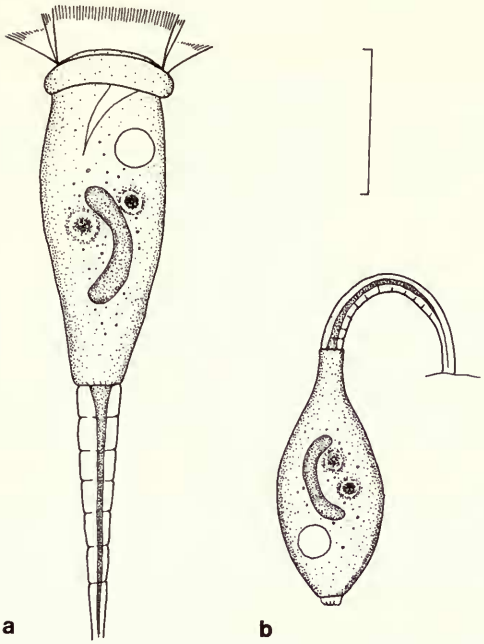

Fig. 8 *Haplocaulus crassicaulis,* (a) relaxed zooid; (b) contracted zooid, composite after Kent, 1881 (called *Vorticella crassicaulis*) and Nenninger, 1948. Bar = 25 μm.

HABITAT. Freshwater, originally found attached to mosses.

NOTE. It is unclear whether the 'fibre' in the lower part of the stalk is an extension of the spasmoneme, or a separate structure. In the case of the latter, it may be necessary to transfer this species to the genus *Monintranstylum.*

Haplocaulus conosomus (Stokes, 1889) n. comb.

Vorticella conosoma Stokes, 1889
Vorticella conesoma Gajewskaja, 1933

DESCRIPTION (Fig. 7). Zooid conical and elongate, 75 μm long × 30 μm wide, and with a distinct ridge in the region of the telotroch band. Peristomial lip 35 μm in diameter. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped or irregular, and situated either centrally or in the anterior part of the body. Pellicular striations visible on zooid. Stalk 150–200 μm long.

HABITAT. Freshwater.

NOTE. In his original description, Stokes (1889) did not describe the spasmoneme. According to Gajewskaja (1933), however, the spasmoneme terminates in the upper part of the stalk. If spasmoneme length is accepted as a generic character, it may be necessary to transfer this species to the genus *Monintranstylum.*

Haplocaulus crassicaulis (Kent, 1881) Stiller, 1971

Vorticella crassicaulis Kent, 1881

DESCRIPTION (Fig. 8). Zooid elongate, 45–50 μm long × 25 μm wide. Peristomial lip 20 μm in diameter. Contractile vacuole situated in upper one-third of body. Macronucleus C-shaped and situated in centre of zooid. Stalk × 1— × 2 body length. Stalk sheath has several transverse folds.

HABITAT. Freshwater, originally isolated as an epizoite of the crustacean *Asellus aquaticus.*

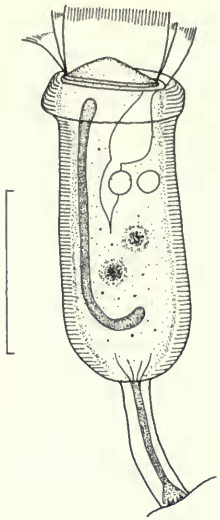

Fig. 9 *Haplocaulus dipneumon*, after Penard, 1922 (called *Vorticella dipneumon*). Bar = 25 μm.

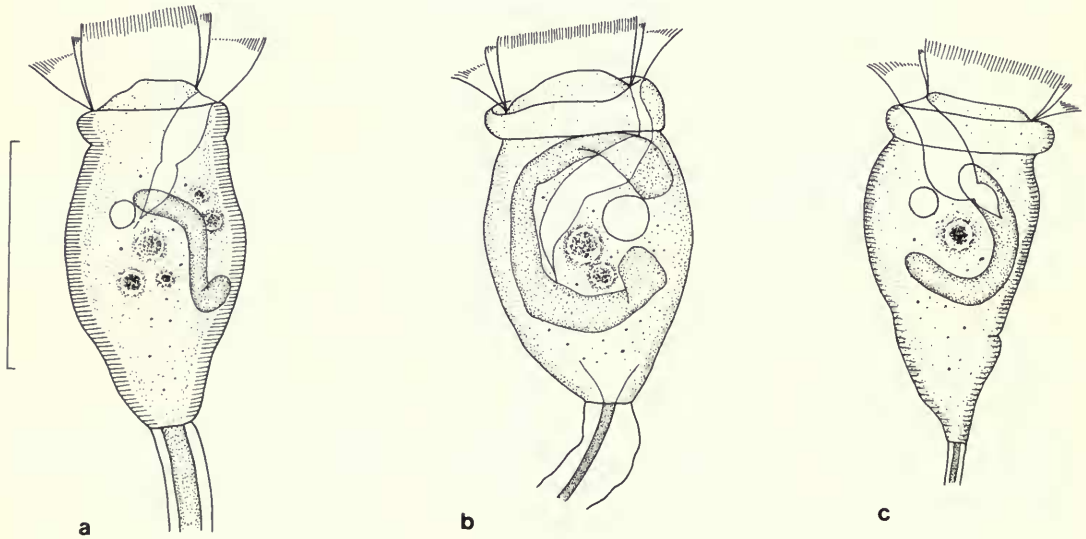

Fig. 10 *Haplocaulus distinguendus*, (a) after Sommer, 1951; (b) after Bierhof & Roos, 1976 (called *Haplocaulus distinguendis)*; (c) after Lüpkes, 1976 (called *Haplocaulus hengsti)*. Bar = 50 μm.

Haplocaulus dipneumon (Penard, 1922) Stiller, 1971

Vorticella dipneumon Penard, 1922

DESCRIPTION (Fig. 9). Zooid almost cylindrical in shape, 50–56 μm long × 25 μm wide. Peristomial lip well developed, 25–30 μm in diameter. Disc convex and raised centrally to a point. Infundibulum almost reaches centre of zooid. Two contractile vacuoles situated in upper one-third of body. Macronucleus elongate and lies

longitudinally with respect to the major body axis. Transverse striations visible on pellicle. Stalk less than body length. Spasmoneme flared at either end.

HABITAT. Freshwater, originally found as an epizoite of the crustacean *Gammarus pulex*.

NOTE. This species bears a strong morphological resemblance to *Baikalonis*. Until its mode of contraction has been described, however, *H. dipneumon* should remain in the genus *Haplocaulus*.

Haplocaulus distinguendus Sommer, 1951

Haplocaulus distinguendis (Sommer, 1951) Bierhof & Roos, 1976
H. hengsti Lüpkes, 1976

DESCRIPTION (Fig. 10). Zooid ovoid, 60–79 μm long × 34–49 μm wide, and constricted beneath peristome. Peristomial lip well developed, 27–40 μm in diameter. Disc convex. Infundibulum broad and reaches almost to centre of body. Contractile vacuole situated in upper half of zooid. Macronucleus irregular or C-shaped. Transverse pellicular striations visible on zooid. Stalk up to 190 μm long × 7·0–9·0 μm wide.

HABITAT. Freshwater, attached to the river weed *Enteromorpha intestinalis* (Sommer 1951), to inanimate substrates (Lüpkes, 1976), and to the crustaceans *Asellus aquaticus* (Sommer, 1951) and *Gammarus* spp. (Bierhof & Roos, 1976).

NOTE. *H. hengsti* is synonymysed with *H. distinguendus* because of their morphological similarity. The main differences between the two are the size of the zooid, *H. hengsti* (79 μm) being slightly longer than *H. distinguendus* (60–75 μm), and stalk length (*H. distinguendus* up to 190 μm long: *H. hengsti*—less than body length). Neither of these characters are particularly reliable for separating species, and there are insufficient differences here to recognise the two as separate taxa.

Haplocaulus eforianus (Tucolesco, 1962) n. comb

Vorticella eforiana Tucolesco, 1962

DESCRIPTION (Fig. 11). Zooid 55–60 μm long × 20 μm wide. Upper part of body cylindrical in shape, lower part conical. Peristomial lip 20–25 μm in diameter. Pellicle with transverse striations, and convex ribbing between the striations. Pellicle also ornamented with numerous knob-like projections. Stalk × 1–× 2 body length.

HABITAT. Marine

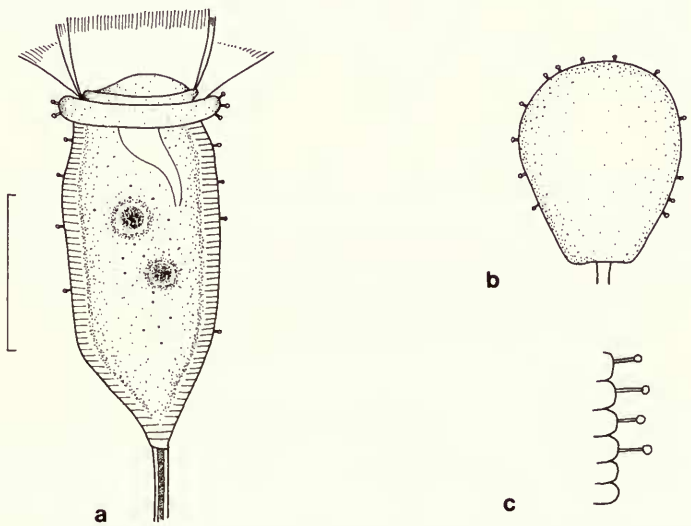

Fig. 11 *Haplocaulus eforianus*, (a) relaxed zooid; (b) contracted zooid; (c) pellicle, showing convex ribbing and knob-like projections, after Tucolesca, 1962 (called *Vorticella eforiana*). Bar = 25 μm.

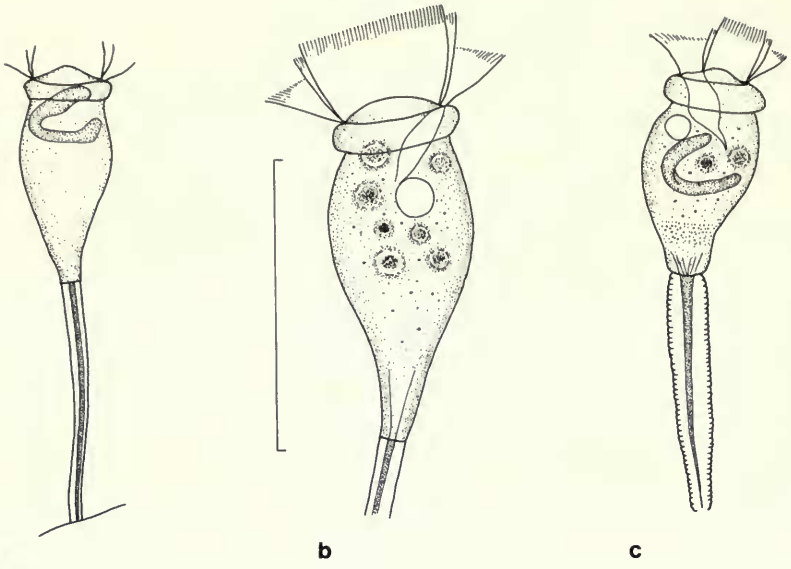

Fig. 12 *Haplocaulus elegans* (a) showing macronucleus; (b) relaxed zooid, after Nenninger, 1948 (called *Vorticella elegans);* (c) after Szczepanowski, 1978. Bar = 50 μm.

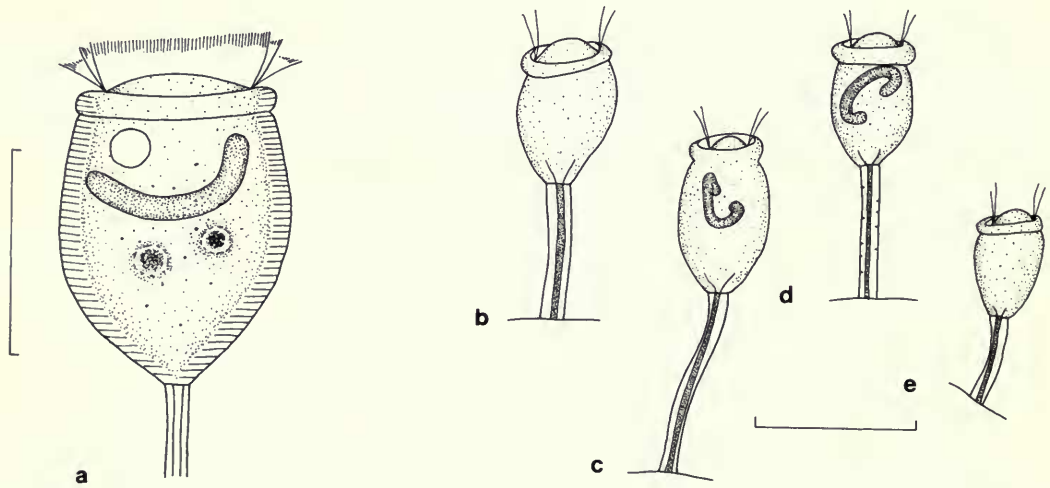

Fig. 13 *Haplocaulus epizoicus* (a) after Sramek-Husek, 1948 (called *Vorticella epizoica),* bar = 25 μm; (b)–(e) after Piesik, 1975, bar = 25 μm.

Haplocaulus elegans (Nenninger, 1948) Stiller, 1971

Intranstylum elegans Nenninger, 1948
Haplocaulus elegans f. gammari Piesik, 1975

DESCRIPTION (Fig. 12). Zooid 42–84 μm long, constricted beneath the peristome and tapering posteriorly towards the stalk. Diameter of peristomial lip less than maximum body width. Disc convex. Contractile vacuole situated in upper one-third of zooid. Macronucleus C-shaped and lies horizontally in the anterior part of the body. Pellicular striations not observed. Stalk × 1– × 2 body length.

HABITAT. Freshwater, originally found attached to the crustaceans *Asellus aquaticus* and *Cyclops* sp.

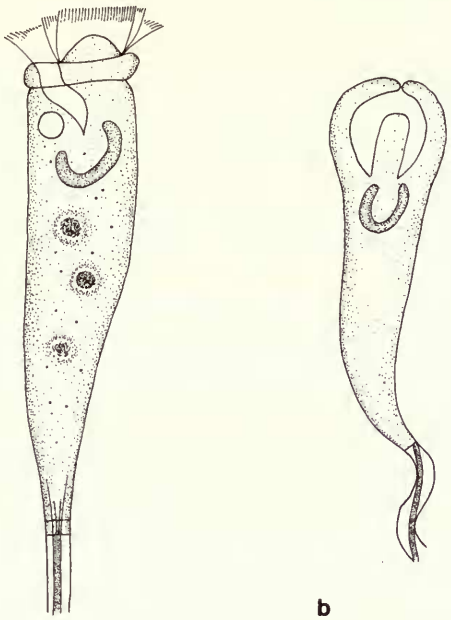

Fig. 14 *Haplocaulus extensus* (a) relaxed zooid; (b) contracted zooid, after Kahl, 1935 (called *Vorticella extensa*). Bar = 50 μm.

Haplocaulus epizoicus (Sramek-Husek, 1948) Stiller, 1971

Vorticella epizoica Sramek-Husek, 1948

DESCRIPTION (Fig. 13). Zooid 25–46 μm long × 18–37 μm wide, inverted bell-shaped and rounded posteriorly. Diameter of peristomial lip about equal to maximum body width. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped and lies either horizontally or obliquely in the anterior part of the zooid. Pellicle with fine transverse striations. Stalk × 1– × 2 body length.

HABITAT. Freshwater, found as an epizoite of the crustaceans *Megacyclopsis viridis* (Sramek-Husek, 1948) and *Gammarus pulex fossarum* (Piesik, 1975).

Haplocaulus extensus (Kahl, 1935) Sommer, 1951

Vorticella extensa Kahl, 1935

DESCRIPTION (Fig. 14). Zooid elongate, 50–100 μm long × 15–27 μm wide (Kahl (1935) described two morphological forms of this species, one 90–100 μm the other 50–70 μm long). Peristomial lip 35 μm in diameter. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped and lies transversely in anterior part of zooid. Pellicle with fine transverse striations. Stalk up to 200 μm long.

HABITAT. Freshwater, found by Sommer (1951) attached to the river weed *Enteromorpha intestinalis*.

Haplocaulus fluviatilis Shubernetskij & Chorik, 1977

DESCRIPTION (Fig. 15). Zooid barrel-shaped with broadened scopular region, 28–48 μm (mean 38 μm) long × 14–30 μm (mean 22 μm) wide. Peristomial lip 17–25 μm (mean 21 μm) in diameter. Disc elevated at angle to peristome and raised centrally to a point. Infundibulum reaches one-third body length. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped and lies horizontally across upper part of zooid. Pellicle with distinct transverse striations, and convex ribbing between the striations. Stalk up to 50 μm long.

HABITAT. Freshwater, originally found attached to the ostracod *Heterocypris*.

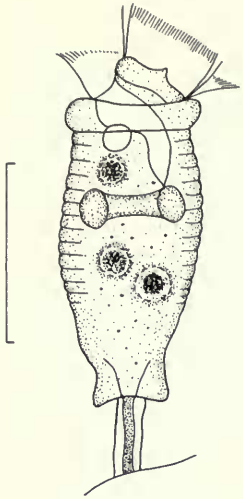

Fig. 15 *Haplocaulus fluviatilis*, after Shubernetskij & Chorik, 1977. Bar = 25 μm.

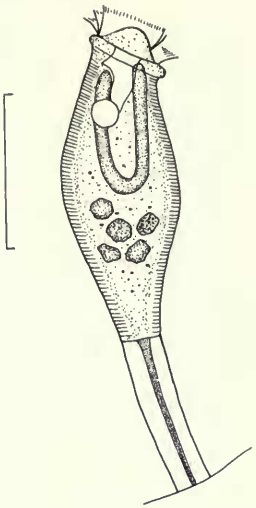

Fig. 16 *Haplocaulus fusiformis*, after Nenninger, 1948 (called *Vorticella fusiforma*). Bar = 75 μm.

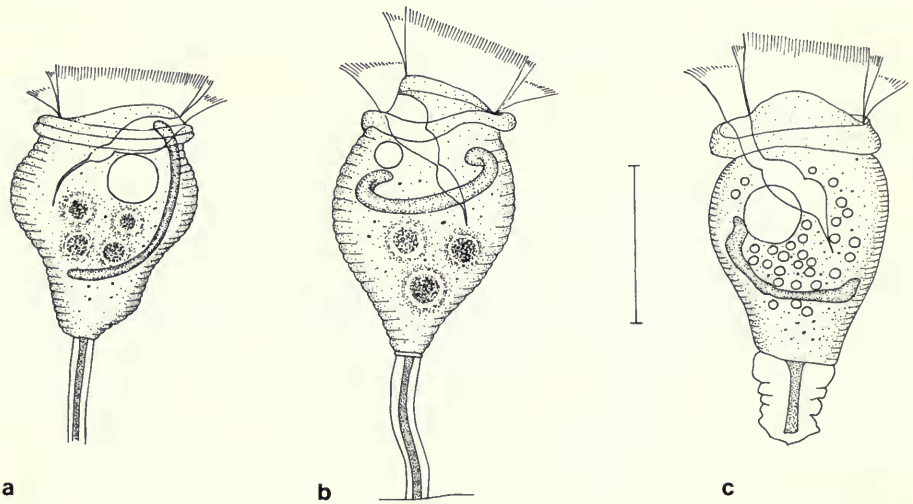

Fig. 17 *Haplocaulus kahlii* (a) & (b) after Stiller, 1931 (called *Vorticella kahlii*); (c) after Bierhof & Roos, 1976. Bar = 25 μm.

Haplocaulus fusiformis (Nenninger, 1948) Stiller, 1971

Vorticella fusiforma Nenninger, 1948

DESCRIPTION (Fig. 16). Zooid 140–162 μm long × 60 μm wide, spindle-shaped with prominent central bulge. Peristomial lip 45 μm in diameter. Disc prominent and conical in shape. Infundibulum reaches one-quarter body length. Contractile vacuole situated in upper one-third of zooid. Macronucleus U-shaped and lies in anterior half of body. Food vacuoles large, dark and hexagonal in shape. Fine transverse striations visible on pellicle. Stalk less than body length.

HABITAT. Freshwater, originally found attached to the tails of tadpoles.

NOTE. Food vacuoles are not accepted as a taxonomic character among the Vorticellidae (Noland & Finley, 1931; Warren, 1986) or, indeed, the rest of the phylum Ciliophora.

Haplocaulus kahlii (Stiller, 1931) Sommer, 1951

Vorticella kahlii Stiller, 1931

DESCRIPTION (Fig. 17). Zooid pyriform with prominent bulge in anterior region, 32–44 μm long × 24–36 μm wide. Peristomial lip well developed, occasionally with central furrow giving the appearance of a double lip. Diameter of lip less than maximum body width. Macronucleus elongate, variable in shape. Pellicle distinctly striated with convex ribbing between striations. Stalk equal to or less than body length.

HABITAT. Freshwater, found as an epizoite of the crustaceans *Leptodora kindlii*, *Daphnia longispina* var *hyalina* and *Salpinia* sp. (Stiller, 1931), *Megacyclopsis viridis* (Sramek-Husek, 1948), and *Gammarus tigrinus* (Bierhof & Roos, 1976).

Haplocaulus leanderi Stiller, 1968

DESCRIPTION (Fig. 18). Zooid inverted bell-shaped, 30–32 μm long × 22–24 μm wide. Peristomial lip well developed, 26–28 μm in diameter. Infundibulum reaches one-third body length. Macronucleus C-shaped and lies horizontally in anterior half of body. Pellicle furnished with numerous small granules. Stalk × 1– × 2 body length.

HABITAT. Marine, originally isolated as an epizoite of the crustacean *Leander* sp.

Haplocaulus longinuclei Banina, 1982

DESCRIPTION (Fig. 19). Zooid 43–61 μm long × 41–49 μm wide, somewhat variable in shape but usually oval or spherical and tapering sharply towards the stalk. Diameter of peristomial lip less than maximum body width. Infundibulum reaches centre of zooid. Macronucleus elongate and irregular in shape. Fine transverse striations visible on pellicle. Stalk less than body length.

HABITAT. Freshwater, originally isolated as epizoites of tadpoles of the amphibian *Rana temporaria*.

Haplocaulus macronucleatus (Nenninger, 1948) Stiller, 1971

Vorticella extensa var *macronucleata* Nenninger, 1948

DESCRIPTION (Fig. 20). Zooid elongate almost cylindrical in shape, 91·5 μm long × 35 μm wide. Diameter of peristomial lip about equal to maximum body width. Disc convex and raised centrally to a point. Contractile vacuole small and situated in upper one-third of body. Macronucleus broad, S-shaped and lies longitudinally with respect to major body axis. Pellicular striations not visible. Stalk about equal to body length.

HABITAT. Freshwater, originally isolated as an epizoite of the hexapod *Ephemera vulgata*.

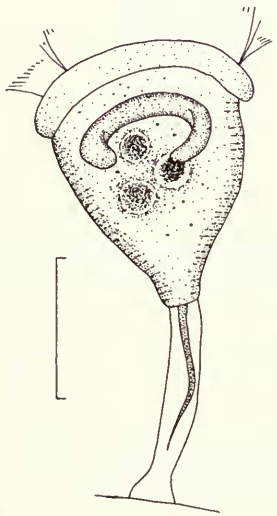

Fig. 18 *Haplocaulus leanderi*, after Stiller, 1968. Bar = 25 μm.

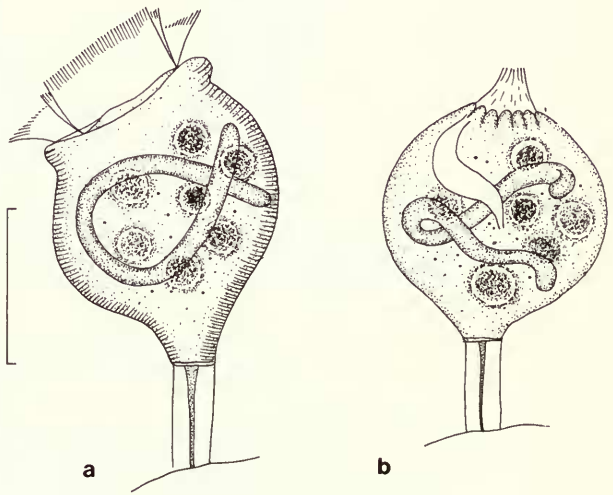

Fig. 19 *Haplocaulus longinuclei* (a) relaxed zooid; (b) contracted zooid, after Banina, 1982. Bar = 25 μm.

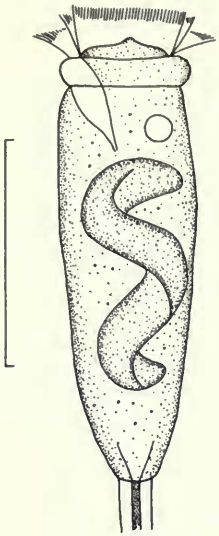

Fig. 20 *Haplocaulus macronucleatus,* after Nenninger, 1948 (called *Vorticella extensa* var. *macronucleata)*. Bar = 50 μm.

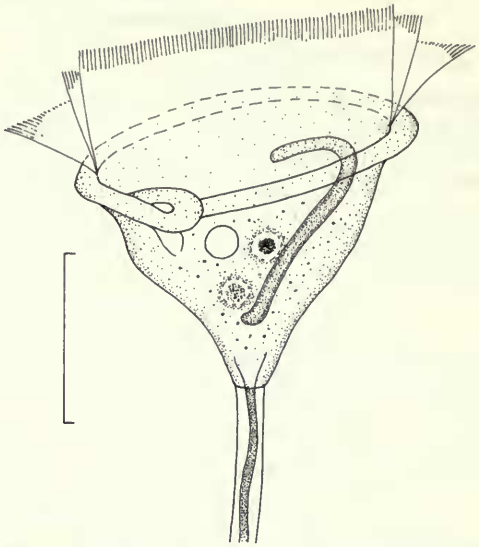

Fig. 21 *Haplocaulus pelagicus,* after Gajewskaja, 1933 (called *Vorticella pelagica)*. Bar = 25 μm.

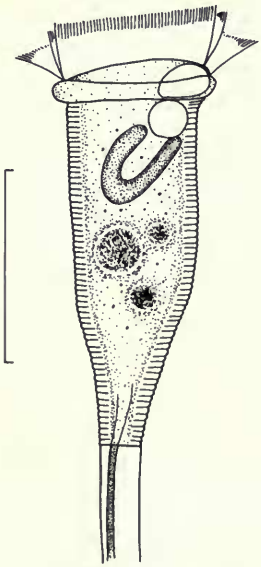

Fig. 22 *Haplocaulus procerus,* after Nenninger, 1948 (called *Vorticella procera)*. Bar = 50 μm.

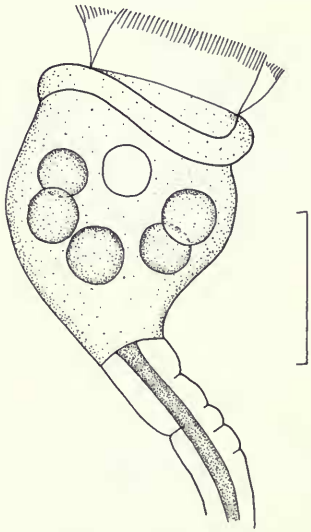

Fig. 23 *Haplocaulus sertulariarum,* after Entz, 1884 (called *Spastostyla sertulariarum)*. Bar = 50 μm.

Haplocaulus pelagicus (Gajewskaja, 1933) Stiller, 1971

Vorticella pelagica Gajewskaja, 1933

DESCRIPTION (Fig. 21). Zooid conical or inverted bell-shaped, 30–40 μm long × 50 μm wide. Peristomial lip 70 μm in diameter. Contractile vacuole situated just below peristome. Macronucleus elongate, irregular in shape and lies longitudinally with respect to major body axis. Pellicular striations not visible. Stalk usually less than body length.

HABITAT. Marine

Haplocaulus procerus (Nenninger, 1948) Stiller, 1971

Vorticella procera Nenninger, 1948

DESCRIPTION (Fig. 22). Zooid elongate, almost cylindrical in shape, 103 μm long × 40 μm wide. Peristomial lip 50 μm in diameter. Disc flat. Contractile vacuole situated just beneath peristomial lip. Macronucleus C-shaped and lies either horizontally or obliquely in the anterior part of the zooid. Food vacuoles typically large. Fine transverse striations visible on pellicle. Stalk × 2–× 3 body length.

HABITAT. Freshwater, originally found attached to the tails of tadpoles. Typically forms pseudocolonies.

Haplocaulus sertulariarum (Entz, 1884) Banina, 1982

Spastostyla sertulariarum Entz, 1884
Vorticella sertulariarum (Entz, 1884) Kahl, 1935

DESCRIPTION (Fig. 23). Zooid inverted bell-shaped, 60–109 μm long × 34–48 μm wide. Diameter of peristomial lip greater than maximum body width. Disc flat. Infundibulum reaches centre of zooid. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped and lies horizontally across centre of anterior part of zooid. Zoochlorellae may be present in cytoplasm. Stalk broad, and equal to or less than body length. Stalk sheath frequently with distinct transverse folds.

HABITAT. Freshwater or marine, originally isolated from the Bay of Naples attached to polyps and sea urchins (Entz, 1884); also found as epizoites of tadpoles of *Rana temporaria*.

NOTE. Entz (1884) considered this organism to be identicle to *Rhabdostyla sertularium* Kent, 1881. *Rhabdostyla sertularium*, however, does not possess a spasmoneme and the stalk is non-contractile whereas Entz's organism clearly has a spasmoneme. *S. sertulariarum* Entz, 1884 was transferred to *Vorticella* by Kahl (1935) and, more recently, to *Haplocaulus* by Banina (1982).

Haplocaulus stilleri Piesik, 1975

DESCRIPTION (Fig. 24). Zooid spindle-shaped, 60 μm long × 27 μm wide, with prominent central bulge. Peristomial lip 20 μm in diameter. Disc convex. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped and lies horizontally across centre of zooid. Pellicular striations not observed. Stalk up to 60 μm long and 12 μm wide.

HABITAT. Freshwater, originally described as an epibiont attached to the crustaceans *Gammarus pulex pulex* (L) and *Gammarus pulex fossarum* (Koch).

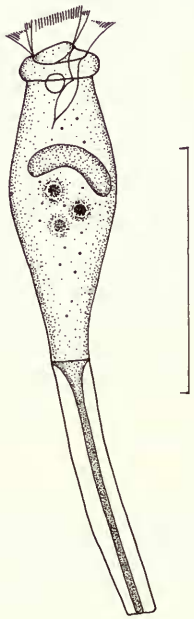

Fig. 24 *Haplocaulus stilleri*, after Piesik, 1975. Bar = 50 μm.

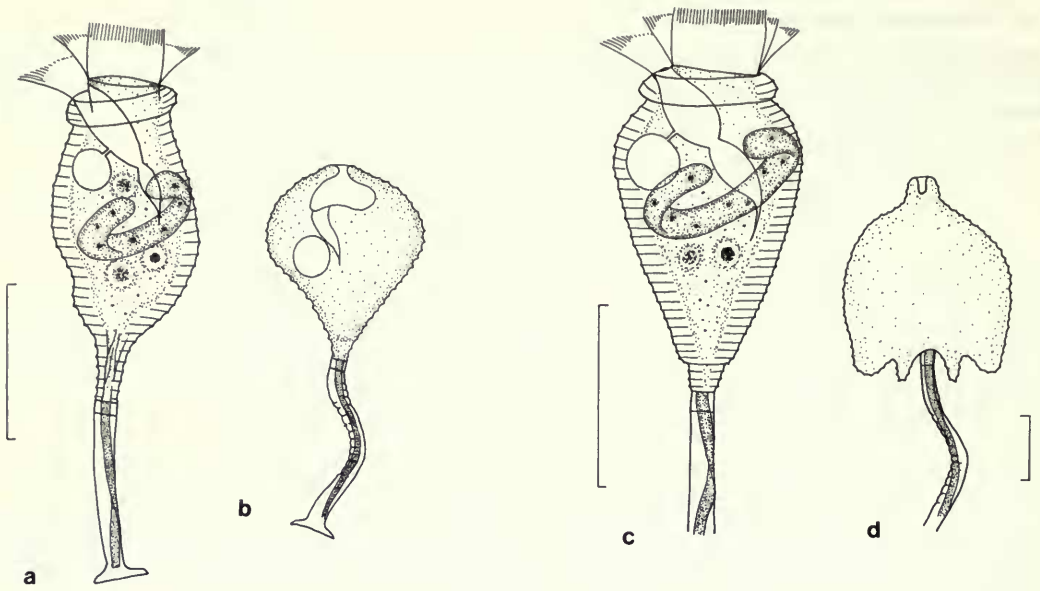

Fig. 25 *Haplocaulus terrenus,* showing variability in relaxed and contracted zooids, (a) relaxed; (b) contracted, bar = 25 μm; (c) relaxed, bar = 25 μm; (d) contracted, bar = 15 μm, after Foissner, 1981.

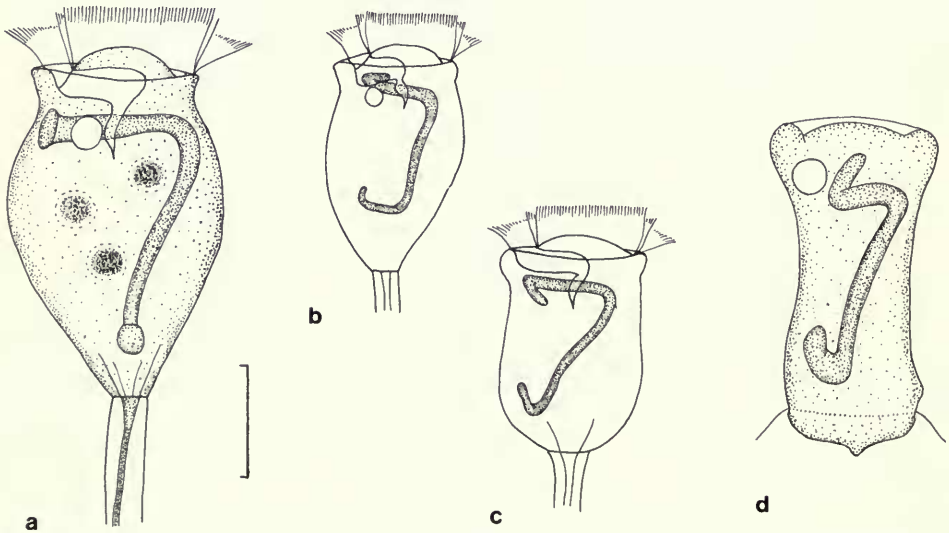

Fig. 26 *Haplocaulus walteri,* (a) typical zooid; (b & c) variations in zooid shape under poor conditions; (d) telotroch, after Guhl, 1985. Bar = 25 μm.

Haplocaulus terrenus Foissner, 1981

DESCRIPTION (Fig. 25). Zooid somewhat variable in shape, 40–60 μm long × 20–26 μm wide. Peristomial lip 20 μm in diameter. Infundibulum reaches centre of zooid. Contractile vacuole large, situated in anterior part of zooid and empties into infundibulum via a short channel. Macronucleus C-shaped and lies either horizontally or obliquely across centre of body. Zooid has 30 transverse striations with concave ribbing between striations. Stalk 2·5–3·5 μm wide, and one-half— × 3 body length. Upon contraction posterior end of zooid may become folded, overlapping the stalk.

HABITAT. Terrestrial, originally isolated from Alpine soils.

Haplocaulus walteri Guhl, 1985

DESCRIPTION (Fig. 26). Zooid 55–75 μm long × 40–60 μm wide, cylindrical to inverted bell-shaped. Diameter of peristomial lip usually less than maximum body width. Infundibulum short. Contractile vacuole situated just below peristome. Macronucleus J- or 7-shaped. Pellicular striations not observed. Stalk up to 158 μm long, and with rod-shaped bacteria attached to the stalk sheath.

HABITAT. Freshwater, originally found in activated sludge.

Genus *BAIKALONIS* Jankowski, 1982

The main distinguishing feature of this genus is the mode of contraction during which the stalk shortens longitudinally and is enveloped by the zooid. When *Baikalonis* was first described (Jankowski, 1982) just one species, *B. foissneri*, was known. *B. foissneri* thus became the type species by monotypy. Two more species, *Vorticella undulata* (Dons, 1918) Noland & Finley, 1931 and *Haplocaulus* sp. Bierhof & Roos, 1976 are here transferred to *Baikalonis*. Three other species of *Haplocaulus, H. amphiurae, H. dipneumon* and *H. fusca*, also bear a strong morphological resemblance to *Baikalonis* although their modes of contraction have yet to be described.

DIAGNOSIS. Solitary, borne upon an unbranched stalk which is typically much shorter than the body. Spasmoneme straight and extends the entire length of the stalk. Upon contraction, the zooid envelopes the stalk which shortens longitudinally.

Key to the species of *Baikalonis*

1 Freshwater; zooid with a contractile vacuole 2
– Marine; zooid without a contractile vacuole . . . . . ***B. undulata***
2 Infundibulum broad and reaches centre of zooid. Contractile vacuole centrally located. Peristomial lip with central furrow . . . . . ***B. foissneri***
– Infundibulum lies diagonally and reaches one-third body length. Contractile vacuole situated just below peristome. Peristomial lip without a furrow . . . . . ***B. gammari***

Species descriptions

Baikalonis foissneri Jankowski, 1982

DESCRIPTION (Fig. 27). This the type species is cylindrical in shape, 56–60 μm long × 20 μm wide. Peristomial lip well developed with central furrow giving the appearance of a double lip. Disc prominently arched above peristome. Infundibulum broad and reaches centre of zooid. Contractile vacuole situated centrally in body. Macronucleus cylindrical in shape and slightly curved. Stalk 12–14 μm long. Spasmoneme broad.

HABITAT. Freshwater, originally found as an epizoite of the larvae of the caddis-fly *Baicalina bellicosa* in Lake Baikal, U.S.S.R.

Baikalonis gammari n. sp.

Haplocaulus sp. Bierhof & Roos, 1976

DESCRIPTION (Fig. 28). Zooid cylindrical in shape, narrowing slightly towards the stalk, 75 μm long × 45 μm wide. Peristomial lip well developed, diameter about equal to maximum body width. Infundibulum reaches one-third body length. Contractile vacuole situated just below peristome. Macronucleus C-shaped and lies longitudinally in centre of zooid. Fine transverse striations visible on pellicle. Stalk 10 μm long × 8 μm wide.

HABITAT. Freshwater, originally isolated as an epizoite of the crustacean *Gammarus pulex*.

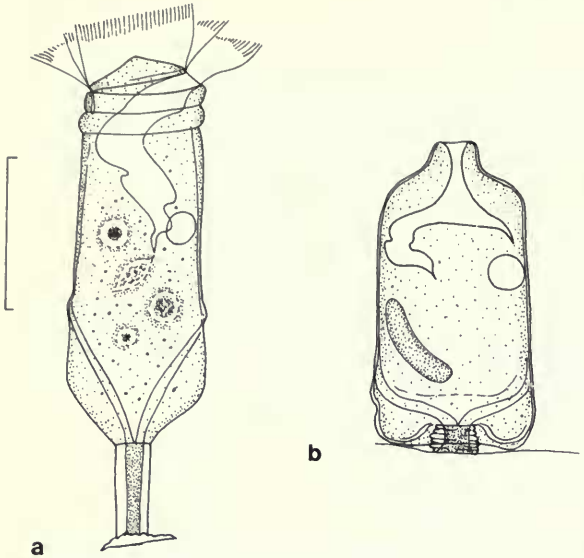

Fig. 27 *Baikalonis foissneri*, (a) relaxed; (b) contracted, after Jankowski, 1982. Bar = 25 μm.

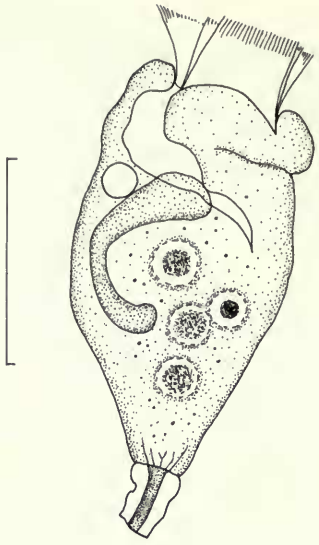

Fig. 28 *Baikalonis gammari*, after Bierhof & Roos, 1976 (called *Haplocaulus* sp.). Bar = 50 μm.

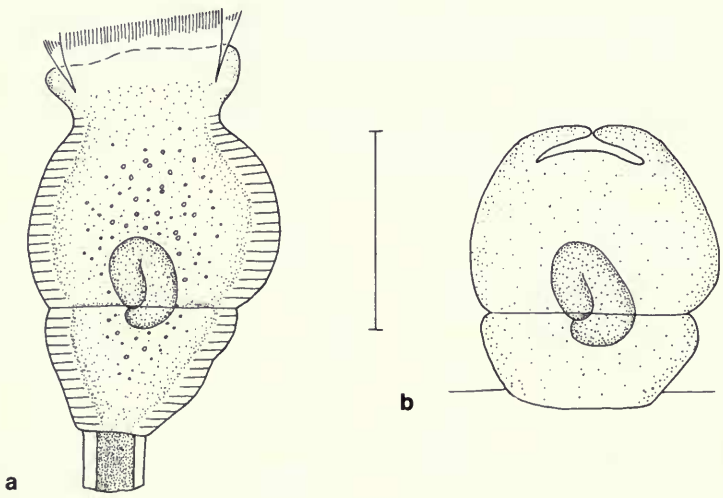

Fig. 29 *Baikalonis undulata*, (a) relaxed; (b) contracted, after Dons, 1918 (called *Vorticellopsis undulata*). Bar = 50 μm.

Baikalonis undulata (Dons, 1918) n. comb.

Vorticellopsis undulata Dons, 1918
Vorticella undulata (Dons, 1918) Noland & Finley, 1931

DESCRIPTION (Fig. 29). Zooid pyriform, 110 μm long × 72 μm wide. Peristomial lip 57 μm in diameter. Two distinct constrictions present on body, one beneath the peristomial lip and the other in the region of the telotroch band. Contractile vacuole not observed. Macronucleus C-shaped, 30 μm long × 20 μm wide and lies longitudinally with respect to major body axis. Transverse striations clearly visible on pellicle. Stalk 115 μm long × 19 μm wide. Spasmoneme 12 μm in diameter.

HABITAT. Marine, originally found attached to the alga *Desmaresita viridis*.

NOTE. Both Noland & Finley (1931) and Kahl (1935) considered that *Vorticellopsis undulata* Dons, 1918 should belong to the genus *Vorticella*. In a recent revision of *Vorticella*, Warren (1986) noted that the stalk of *V. undulata* does not contract spirally and should not, therefore, be included in the genus *Vorticella*. The mode of contraction and the morphology of the stalk both indicate that this species should belong to the genus *Baikalonis*.

Genus ***COTENSITA*** Jankowski, 1982

The main distinguishing feature of the genus *Cotensita* is the stalk sheath which is folded in a characteristic fashion just beneath the zooid. Although some colonial peritrichs such as *Craspedomyoschiston* have ornamentation of the stalk sheath, this feature has not previously been recorded among solitary vorticellids. The spasmoneme of *Cotensita* is straight and extends to about two-thirds of the stalk length. *C. commensalis* Jankowski, 1982 is the type species by monotypy.

DIAGNOSIS. Spasmoneme straight, not extending the full length of the stalk. Stalk sheath twisted in the region just below the stalk. Upon contraction the zooid bends over to one side and assumes a characteristic 'nodding' position.

Species description

Cotensita commensalis Jankowski, 1982

DESCRIPTION (Fig. 30). This the type species is inverted bell-shaped, 46 μm long × 36 μm wide. Diameter of peristomial lip about equal to maximum body width. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped. Stalk 85–90 μm long. Stalk sheath twisted to form 1–2 helical coils just below zooid. Spasmoneme reaches two-thirds stalk length with the posterior end tapering to a point.

HABITAT. Freshwater, originally isolated as an epizoite of the larvae of the caddis-fly *Baicalina bellicosa* from Lake Baikal, U.S.S.R.

Genus ***PARAZOOTHAMNIUM*** Piesik, 1975

The main distinguishing feature of this genus is the mode of stalk contraction which takes place in two stages: initially the stalk shortens longitudinally in a concertina-like fashion but, if the stimulus is sufficiently strong, it loops and bends in the more usual manner.

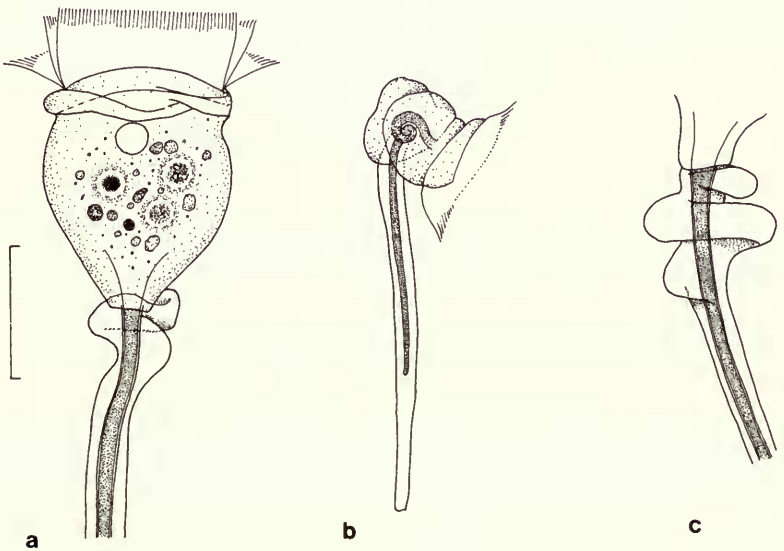

Fig. 30 *Cotensita commensalis*, (a) relaxed zooid, bar = 25 μm. (b) partially contracted; (c) detail of stalk, after Jankowski, 1982.

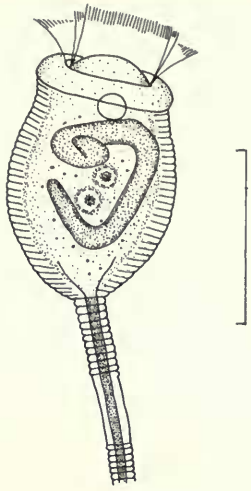

Fig. 31 *Parazoothamnium stenotica,* after Piesik, 1975. Bar = 50 μm.

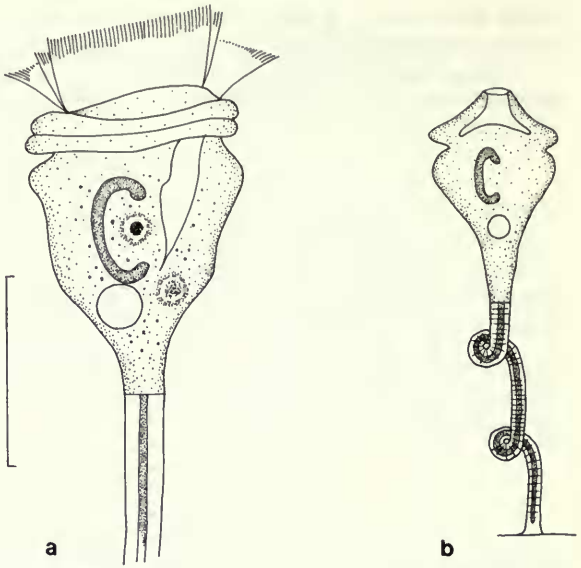

Fig. 32 *Parazoothamnium claparedei,* (a) relaxed zooid; (b) contracted, after Andrussowa, 1886 (called *Vorticella claparedei).* Bar = 50 μm.

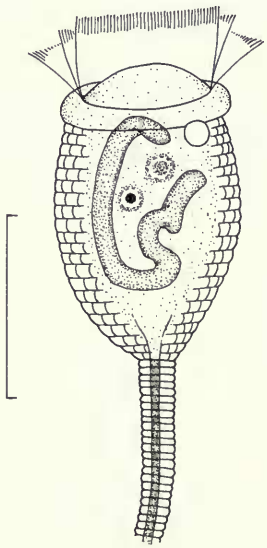

Fig. 33 *Piesika gammari,* after Piesik, 1975 (called *Parazoothamnium gammari).* Bar = 50 μm.

Piesik (1975) originally described two species of *Parazoothamnium, P. stenotica* and *P. gammari.* The latter species, however, has rows of regularly arranged tubercles and, since this is recognised as a generic character among the Vorticellidae, *P. gammari* is transferred to the new genus *Piesika. P. claparedei* is included in the genus *Parazoothamnium* for the first time. *P. stenotica* is designated the type species.

DIAGNOSIS. Solitary, borne upon an unbranched stalk. Spasmoneme extends the complete length of the stalk. Stalk contraction takes place in two stages; initially it shortens longitudinally in a

concertina-like fashion but, if the stimulus is sufficiently strong, it loops and folds. Zooid has a transverse silverline system.

Key to the species of *Parazoothamnium*

1 Macronucleus J-shaped; contractile vacuole situated in anterior half of body . ***P. stenotica***
– Macronucleus C-shaped; contractile vacuole situated in posterior half of body . ***P. claparedei***

Species descriptions

Parazoothamnium stenotica Piesik, 1975

DESCRIPTION (Fig. 31). This the type species is inverted bell-shaped, somewhat rotund, 70 μm long × 50 μm wide. Peristomial lip well developed, diameter about equal to maximum body width. Contractile vacuole situated just beneath peristome. Macronucleus J-shaped. Pellicle with fine transverse striations. Stalk up to 9·0 μm wide.

HABITAT. Freshwater, originally isolated as an epizoite of the crustacean *Gammarus pulex*.

Parazoothamnium claparedei (Andrussowa, 1886) n. comb.

Vorticella claparedei Andrussowa, 1886

DESCRIPTION (Fig. 32). Zooid campanulate, 85 μm long × 60 μm wide and with a distinct swelling just below the peristome. Peristomial lip 60 μm in diameter and with a central furrow to give the appearance of a double lip. Disc raised obliquely above peristome. Infundibulum reaches centre of zooid. Single contractile vacuole situated in posterior half of zooid. Macronucleus C-shaped and lies longitudinally with respect to major body axis. Pellicular striations not observed. Upon contraction stalk sheath assumes a wrinkled appearance and stalk coils into two or three unevenly spaced loops.

HABITAT. Marine, attached to filamentous algae.

Genus ***PIESIKA*** n. gen.

The possession of regularly arranged pellicular tubercles along with an underlying reticulate silverline system is regarded as a generic character among peritrichs (Foissner & Schiffmann, 1974; Warren, 1986). The genus *Piesika* is erected to include solitary vorticellids which both possess pellicular tubercles, and exhibit the two stage stalk contraction process seen in *Parazoothamnium*. *P. gammari* is the type species by monotypy.

DIAGNOSIS. Solitary zooids borne upon an unbranched stalk. Spasmoneme extends the complete length of the stalk. Contraction of the stalk takes place in two stages; initially the stalk shortens longitudinally in a concertina-like fashion but, if the stimulus is sufficiently strong, it loops and folds. Zooid with rows of regularly aligned pellicular tubercles.

Species description

Piesika gammari (Piesik, 1975) n. comb.

Parazoothamnium gammari Piesik, 1975

DESCRIPTION (Fig. 33). This the type species is inverted bell-shaped, 70 μm long × 50 μm wide. Diameter of peristomial lip about equal to maximum body width. Disc convex. Contractile vacuole situated just below peristome. Macronucleus elongate and irregular in shape. Stalk up to 240 μm long × 10 μm wide. Cysts nearly spherical in shape, 49 μm × 43 μm.

HABITAT. Freshwater, originally found as an epizoite of the crustacean *Gammarus pulex pulex*.

Genus ***PSEUDOHAPLOCAULUS*** n. gen.

Foissner & Schiffmann (1974) reported that two types of silverline system are found among vorticellids; (i) transverse, in which the lines encircle the body in one direction only, and (ii) reticulate, which consists of a network of vertical and horizontal lines. Furthermore, it has been established that vorticellids with regularly arranged rows of pellicular tubercles also possess reticulate silverline systems (Foissner, 1979, 1981; Carey & Warren, 1983; Warren, 1987). The genus *Pseudohaplocaulus* is erected to include *Haplocaulus*-like peritrichs which possess rows of regularly aligned pellicular tubercles and, therefore, reticulate silverline systems. There are two species of

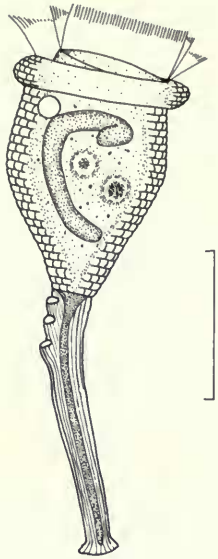

Fig. 34 *Pseudohaplocaulus nicoleae*, after Precht, 1935 (called *Haplocaulus nicoleae*). Bar = 25 μm.

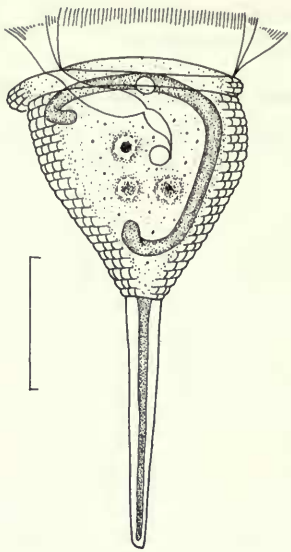

Fig. 35 *Pseudohaplocaulus anabaenae*, after Stiller, 1940 (called *Vorticella anabaenae*). Bar = 25 μm.

Pseudohaplocaulus, both formerly belonging to the genus *Haplocaulus*. *Pseudohaplocaulus nicoleae* (Precht, 1935) n. comb. is the type species.

DIAGNOSIS. Solitary, borne upon an unbranched stalk that is circular in cross-section and contracts in a zigzag manner. Zooid with rows of regularly aligned pellicular tubercles and a reticulate silverline system.

Key to species of *Pseudohaplocaulus*

1	Marine. Zooid with one contractile vacuole	***P. nicoleae***
–	Freshwater. Zooid with two contractile vacuoles	***P. anabaenae***

Species descriptions

Pseudohaplocaulus nicoleae (Precht, 1935) n. comb.

Haplocaulus nicoleae Precht, 1935

DESCRIPTION (Fig. 34). This the type species is inverted bell-shaped, 35–40 μm long × 25 μm wide. Peristomial lip 30 μm in diameter. Contractile vacuole situated just below the peristome. Macronucleus J-shaped. Stalk × 1– × 2 body length. Sites of previous zooid division may be visible as short lateral extensions of the stalk sheath (see Fig. 34).

HABITAT. Marine, originally found as an epizoite of the polychaete, *Nicolea zostericola*.

Pseudohaplocaulus anabaenae (Stiller, 1940) n. comb.

Vorticella anabaenae Stiller, 1940
Haplocaulus anabaenae Stiller, (1940) 1971

DESCRIPTION (Fig. 35). Zooid inverted bell-shaped, 40–45 μm long × 40 μm wide. Peristomial lip 45 μm in diameter. Disc flat. Infundibulum reaches one-third body length. Two contractile vacuoles, one situated near the base of the infundibulum, the other just below the peristome. Macronucleus J-shaped. Stalk × 1– × 2 body length.

HABITAT. Freshwater, originally isolated as an epibiont attached to the Cyanobacterium *Anabaena*.

Incertae Sedis

Genus *MONINTRANSTYLUM* Banina, 1977

Monintranstylum is a solitary peritrich the stalk of which contracts in a zigzag rather than helical fashion. The main distinguishing feature of *Monintranstylum* is the spasmoneme which is short and terminates above the base of the stalk, unlike that of *Haplocaulus* and other related genera where the spasmoneme is usually about the same length as the stalk.

Spasmoneme length has long been recognised as a generic character among colonial peritrichs. *Intranstylum* Fauré-Fremiet, 1904, for example, differs from *Carchesium* Ehrenberg, 1830 by the absence of the spasmoneme in the central trunk of the stalk. *Myoschiston* Precht, 1935 may similarly be recognised from *Zoothamnium* Bory, 1826. Among the solitary peritrichs, however, the situation is less clear and several species belonging to genera in which the whole stalk is normally contractile, have short or otherwise incomplete spasmonemes. The spasmoneme of *Vorticella intermissa* Nenninger, 1948, for example, begins a short distance below the scopula and is therefore absent in the uppermost part of the stalk; and in *Haplocaulus claudicans* a small 'fibre' connects the short spasmoneme to the stalk base (see p. 132). Furthermore, the author has frequently observed both solitary and colonial peritrichs in which the spasmoneme appears to have partially degenerated and lost its contractility (unpublished data). Clearly, further research is necessary before spasmoneme length can be accepted as a generic character among solitary peritrichs.

NOTE. The name *Monintranstylum* was first mentioned in an abstract (Banina, 1976). A full description of *Monintranstylum*, however, did not appear until the following year (Banina, 1977*a*), the date from which the genus should properly be recognised. The first named species of *Monintranstylum* were described in a second article later in the same journal (Banina, 1977b). No type species was designated.

DIAGNOSIS. Zooid borne upon a stalk which contracts in a zigzag manner. Solitary, never colonial, and carried upon an unbranched stalk. Spasmoneme present only in the upper part of the stalk.

Species of *Monintranstylum*

Three species of *Monintranstylum* were described by Banina (1977*b*), *M. rotundus*, an epibiont of *Daphnia longispina; M. stammeri*, an epibiont of *Polyphemus pediculus, Daphnia pulex, Ceriodaphina quadrangulata* and *Cyclops* sp.; and *M. sommeri* on the abdomen of *Eucyclops serrulatus* and the shell of *Cypris* sp. The original descriptions of these species were not available for this revision.

Banina (1982) also transferred *Intranstylum ranae* Stiller, 1953 to the genus *Monintranstylum* on the basis that *I. ranae* is solitary rather than colonial, and that its spasmoneme terminates above the base of the stalk. However, for the reasons given above, *M. ranae* and the three other species of *Monintranstylum* may perhaps more properly belong to the genus *Haplocaulus*.

Monintranstylum ranae (Stiller, 1953) Banina, 1982

Intranstylum ranae Stiller, 1953

DESCRIPTION (Fig. 36). Zooid 65–90 μm long × 35–50 μm wide. Diameter of peristomial lip usually less than the maximum body width. Contractile vacuole situated just below the peristome. Macronucleus variable, usually S-shaped. Pellicle with fine transverse striations. Stalk up to × 3 body length. Stalk base flattened to form a large attachment area, the diameter of which often exceeds that of the body.

HABITAT. Freshwater, attached to the tail fins of frog tadpoles.

Genus *TUCOLESCA* (Tucolesco, 1962) Lom in Corliss, 1979

Leptodiscus Tucolesco, 1962.

The main distinguishing features of this genus are (i) the reported absence of a peristomial lip, and (ii) upon contraction, the peristome remains open with the cilia extended while the stalk folds into several (usually three) loose coils. *T. mirabilis* is the type species by monotypy.

The name originally assigned to this genus was *Leptodiscus*, a homonym of the dinoflagellate

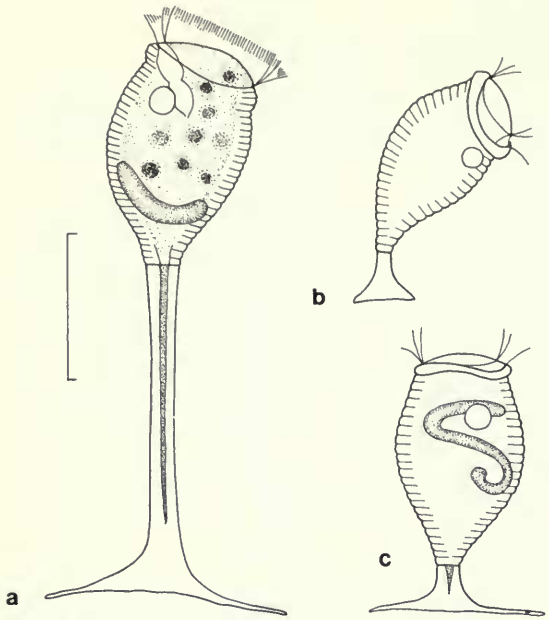

Fig. 36 *Monintranstylum ranae,* (a) typical form; showing variability of (b) zooid, and (c) macronucleus, after Stiller, 1953 (called *Intranstylum ranae).* Bar = 50 μm.

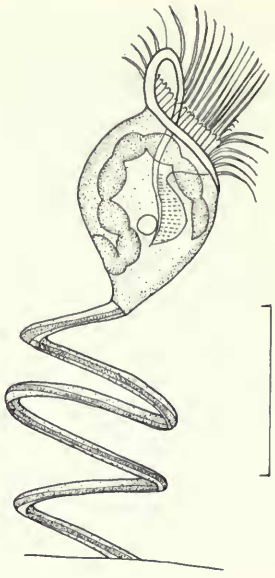

Fig. 37 *Tucolesca mirabilis,* after Tucolesco, 1962 (called *Leptodiscus mirabilis).* Bar = 25 μm.

Leptodiscus Hartwig, 1877 (Corliss, 1979). The genus was renamed *Tucolesca* by Lom (unpublished—see Corliss, 1979). The taxonomic status of the genus and validity of the name are both considered doubtful.

DIAGNOSIS. Zooid with long, prominent cilia and without a peristomial disc. Upon contraction, peristome remains open with the cilia extended while the stalk is folded into several loose coils.

Species description

Tucolesca mirabilis (Tucolesco, 1962) Lom

Leptodiscus mirabilis Tucolesco, 1962

DESCRIPTION (Fig. 37). Zooid 27–30 μm long × 19 μm wide. Peristomial lip 20 μm in diameter and obliquely orientated with respect to major body axis. Cilia 16–19 μm long. Infundibulum reaches two-thirds of the body length. Contractile vacuole located near base of infundibulum. Macronucleus S-shaped and moniliform. Stalk up to 80 μm long.

HABITAT. Originally isolated from Lake Tekirghiol, a saline lake in Romania.

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